

OBSERVATIONS ON  
THE HETEROMI, AN ORDER OF  
TELEOST FISHES



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# OBSERVATIONS ON THE HETEROMI, AN ORDER OF TELEOST FISHES

By N. B. MARSHALL

## INTRODUCTION

THE order Heteromi was introduced by Gill (1899, pp. 1016-1017) as a sanctuary for fishes of the genus *Notacanthus*. Gill made his decision perfectly plain: "The genus *Notacanthus* has long been shifted from place to place without finding a natural resting-place. It was indeed long ago suggested by Dr. Günther that 'these fishes will, no doubt, have to be placed in a distinct order'; but he has neglected to do so, or to give any reasons why he thought so. The facts now known, however, warrant the isolation suggested, and the order may now be defined by the following characteristics". Such "facts" are out of place here, but it is relevant to consider another order introduced and defined by Gill immediately before the Heteromi. This is the order Lyopomi (Gill, 1899, pp. 1015-1016), proposed to hold the family of halosaurid fishes, another group of deep-sea species' . . . approximated by most ichthyologists to the Notopterids and Alepocephalids and their supposed allies".

When revising the Heteromi (as defined by Gill), Goode and Bean (1895) proposed three new genera, *Gigliolia*, *Macdonaldia* and *Lipogenys*. The last was made the generic type of a new family, Lipogenyidae, which had been proposed and defined by Gill (M.S.). The Lipogenyidae are clearly distinct from the Notacanthidae in having a toothless, suctorial mouth and a short-based dorsal fin, composed half of spines and half of rays. It was the last feature that led Boulenger (1904) to the following decision: "The recent discovery of a third family, the Lipogenyidae, which in the structure of the dorsal fin, is exactly intermediate between the two others, has lessened the gap between the Lyomeri (*sic*) (Halosauridae) and Heteromi (Notacanthidae) of Gill, which I have proposed to write in a suborder under the latter name". Boulenger also regarded the Dercetidae and Fierasferidae as heteromous fishes. Regan (1909, 1910, 1929) followed Boulenger's decision with certain reservations, these being the exclusion of " . . . the Dercetidae, in my opinion probably belonging to the Iniomi, and the Fierasferidae, which are without question specialized Brotulidae" (1909, p. 82). The Heteromi were also given ordinal status.

In his classification of fishes, Berg (1940) has returned to Gill's concept of two separate orders, Halosauriformes (= Lyopomi) and Notacanthiformes (= Heteromi). Berg must have decided that the differences between the two groups were trenchant

enough for ordinal status. But the contention of this paper is that the Heteromi (in Regan's sense) form a natural group, the differences between the halosaurs and notacanthids not being of a radical nature. In particular, the divergences in fin structure are more apparent than real, for some of the spines of the Notacanthidae are intermediate between fully spinous structures and soft rays. Lastly, study of the swimbladders of both halosaurs and notacanthids has revealed close similarities in structural plan. The design of the heteromous swimbladder is also remarkably like that of eels (Apodes), which may well indicate that the two groups diverged from a common ancestor.

#### SOME DIFFERENCES BETWEEN THE HALOSAURID AND NOTACANTHID FISHES

Consideration of the structural differences between the halosaurs and notacanthids, so as to try and see these divergences in better perspective, must obviously precede any attempt to assess the status of the Heteromi. But before this can be done a supposed difference must be eliminated. In defining the order Halosauriformes, Berg, (1940, p. 453), has followed Günther's (1887) description of the anatomy of *Aldrovandia macrochir*, where Günther stated (and showed in Plate LX, fig. 1) that the preoperculum is reduced to a small bone, situated at the lower side of the quadrate. The Notacanthidae have a normal preoperculum and Gill (1889, p. 1015) believed this was also true of the halosaurs. His observations were as follows: "Dr. Günther, in 1868 (*Cat. Fishes*, B.M. vii, 482) assigned to the genus *Halosaurus* a preoperculum produced behind into a long flat process, replacing the sub- and interoperculum. The improbability of such a coalescence of the preoperculum and suboperculum, in view of our knowledge of the genesis and development of these bones, was so extreme that I availed myself of the first opportunity to examine the facts in the case. At Wood's Hole, in 1883, I uncovered the bones sufficiently to detect the true preoperculum, and to recognise that the supposed 'preoperculum' of Günther was the exact homologue of the suboperculum. I deferred publication of any conclusions as to the affinities of the genus, however, till I could examine the skeleton. Meanwhile, a notice and illustration of the skull and scapular arch of the genus have been published by Dr. Günther (*Challenger Deep-Sea Fishes*, pp. 232-236, Pl. 60, figs. 1-8). Dr. Günther at last recognized the true homologues of the opercular apparatus, but has not appreciated the systematic import of the facts disclosed".

But Gill (perhaps in his eagerness to "have at" Günther) did no more than confuse the issue. Günther's (1868, p. 482) original description of the preoperculum of *Halosaurus* is apt in part: "Preoperculum produced behind into a long flat process, replacing the sub- and interoperculum". There is no mention of a coalescence between this bone and the suboperculum. The flat process "replaces" the sub- and interoperculum by providing a framework for the gill cover at a place where these two bones are normally found. [In fact the suboperculum and interoperculum are simply concealed by the backward process of the preoperculum (see Text-fig. 1).]

Having appreciated this unusual preopercular development, it is odd that Günther went so astray in his (1887) Challenger Report. Here Gill missed a fine opportunity for Günther did not recognize the "true homologues of the opercular apparatus". In defining the genus *Halosaurus* (p. 232), Günther described the preoperculum as "rudimentary", the suboperculum as "large" and the interoperculum as "membranous". In Plate LX, fig. 2, the "preoperculum" is shown as a small bone immediately below the quadrate, and is described as such by Günther (p. 235). After examining the skeleton of *Aldrovandia macrochir*, from which figures 1-8 of Plate LX were derived, I found that the "preoperculum" is actually the posterior, well ossified part of the quadrate, which must have become detached from

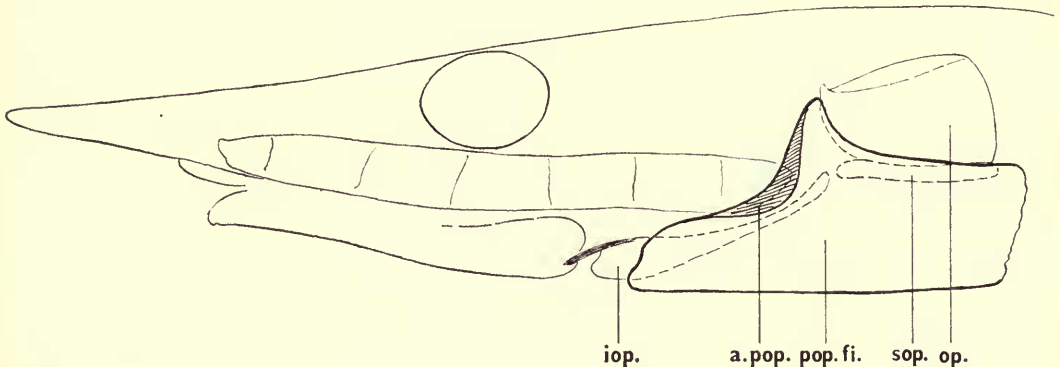


FIG. 1. The head of *Aldrovandia affinis*, showing the gill-cover bones ( $\times 3$ ). The preoperculum has a thickened outline and its anterior part is cross-hatched. A. pop., anterior part of preoperculum; pop. fl., greatly expanded flange of preoperculum; iop., interoperculum; op., operculum; sop., suboperculum.

the fan-shaped, less robust part of this bone. The complete set of gill cover bones in a specimen of *Aldrovandia affinis* may be seen in Text-fig. 1, which shows the anterior part of the preoperculum in the usual position.

Comparison of this figure with Günther's Plate LX, fig. 1, will also show that the bone he labels as the suboperculum is actually the posterior expansion of the preoperculum. This expansion is not a new formation for it carries the (horizontal) continuation of the mandibular lateral line canal, the section that normally turns upwards and curves round the posterior flange of the preoperculum. This flange is generally separated from the more robust anterior part by a ridge, which is also well developed in halosaurids. The extension of the preoperculum is then a greatly expanded posterior flange, a development that is clearly related to the disposition of the sensory canals of the head. In particular, the expansion is keyed to the course of the suborbital canal, which is also unusual. Instead of curving round the orbit, it continues straight backwards and so covers all but a small upper section of the anterior, crescentic part of the preoperculum. The canal tapers to an end on the upper part of the expanded preopercular flange. This being so, there is

clearly no room for the (normal) preopercular extension of the mandibular canal, which can only continue straight backwards, and is floored (in the usual manner) by the preopercular flange: hence the great downward extension of this structure, a striking instance of correlation between neuromast disposition and bony development.

All but the neuromasts on the upper parts of the head are thus concentrated below the longitudinal axis of the body, an arrangement that may well have a special significance for the well-being of halosaurs. Observers in bathyscaphes have seen them hovering over the sediments, keeping station against a current by undulations of the after body. Their visual field must certainly be restricted. Perhaps the ventral housing of the highly developed neuromast organs enhances their reception of water disturbances under the body of the fish, both those caused by swimming crustaceans, etc., and those due to the respiratory currents of animals living in the oozes. (Collett (1896) found a small cephalopod (*Rossia*) in the stomach of an *Aldrovandia macrochir*, while Günther (1887) found shrimp-like crustaceans in a Challenger specimen of this species.)

As already stated, the expanded preopercular flange covers the suboperculum and interoperculum. The suboperculum is reduced to a narrow strip of bone and is linked by a ligament to the upper end of the paddle-shaped interoperculum. This bone runs downwards and forwards beneath the preopercular flange and comes into view at the anterior extremity (see Text-fig. 1), where it is joined by a strong ligament to the angle of the lower jaw. Presumably this interopercular-mandibular coupling plays a part, as in other teleosts, in the opening of the jaws.

In brief, all the opercular bones are formed in a halosaur, but the preoperculum is far from rudimentary. The enormous extension of the preopercular flange, which replaces the suboperculum and interoperculum as a covering bone, is related to the unusual disposition of the suborbital and mandibular lateral line canals.

In the Notacanthidae the head canals and gill cover bones follow the usual teleost pattern. These structural contrasts are thus quite striking, but the differences in opercular ossifications are not so trenchant as formerly supposed. A seemingly radical difference concerns the fin rays, which are soft and jointed in the halosaurs, but in both the Notacanthidae and the Lipogenyidae there are some spines in the anal and pelvic fins. The dorsal fin of *Lipogenys* consists of four or five spines followed by five to seven branched rays. Concerning the Notacanthidae, Goode & Bean (1895) described the dorsal fin as consisting of short and free spines and ". . . with soft rays very few or absent". Regan (1929) also referred to the dorsal spines as "isolated". But in *Notacanthus (sexspinis* and *bonapartei*) and *Macdonaldia (challengeri* and *rostrata*), the dorsal spines are not separate entities: Indeed, there is a strong linkage between the radial (basal) supports of the spines (see Text-fig. 2). Each spine also has its own set of muscles. The dorsal spines may thus be regarded as forming the whole or the greater part of a single dorsal fin. (In *Notacanthus* spp. and *Polyacanthonotus* one or two soft rays may be found behind the last dorsal spine.) This being so, there is the following morphological series in dorsal fin structure: Halosauridae (10-13 rays, short-based); Lipogenyidae (5 spines + 5 rays, short-based); *Notacanthus* (6-12 spines + 1-2 rays,

medium—to long-based); *Polyacanthonotus* (29–37 spines + 1 ray, long-based); *Macdonaldia* (27–34 spines, long-based).

This graded series and the finding that the dorsal spines of the notacanth form most or the whole of a single fin, indicates that the two main groups are less distinct in fin pattern than has been supposed. Scrutiny of the structure of notacanth spines strengthens this impression. In *Notacanthus bonapartei*, for instance, the last (2–5) anal spines show definite signs of segmentation (see Text-fig. 3a). The divisions between the segmentation are quite clear but they may not reach the surface of the spine. The transition from spines to soft rays is nearly always sharp, each segmented spine being pointed and rigid (in two specimens out of ten the last anal “spine” was somewhat flexible). Indeed, there is no outward evidence (or inward, as far as I could see) of the typical double structure found in a soft ray, the leading surfaces being perfectly rounded and smooth. There may be a median

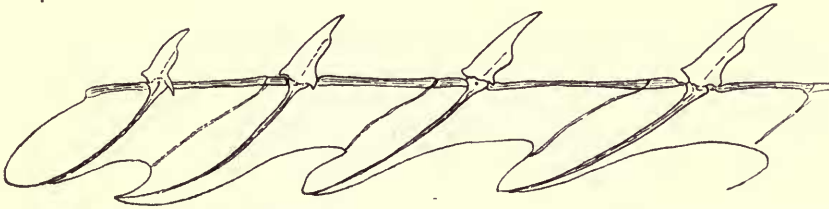
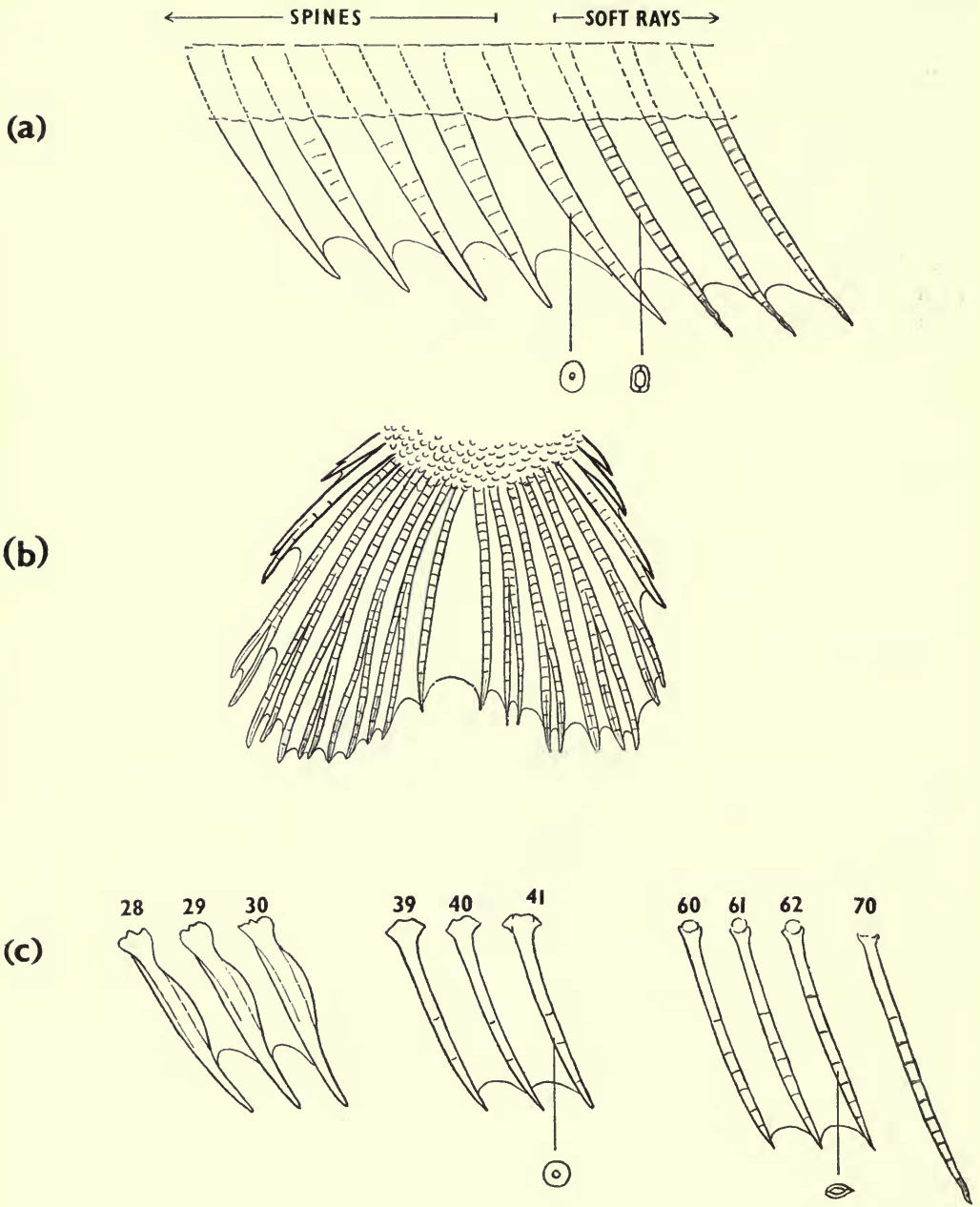


FIG. 2. The first four dorsal spines of *Notacanthus sexspinus*, showing their basal (radial) supporting bones ( $\times 3$ ). The radials fit closely together, but the sutures between them are visible, as shown in the figure.

groove down the lower anterior half of the dorsal spines, but whether this is to be regarded as significant is questionable. Most, perhaps all, of the fin spines of notacanth are hollow and do not seem to be so well ossified as those of a typical percormorph.

Each pelvic fin of *N. bonapartei* has three spines and the innermost (and longest) one is usually segmented. This spine may have another resemblance to a soft ray in being forked at the distal end, as may be seen in Text-fig. 3b. Out of ten specimens examined, seven had this kind of innermost pelvic spine.

The pelvic fins of *Macdonaldia challengerii* and *M. rostrata* each have a small outer spine, which in the specimen of *rostrata* that I examined had to be dissected out under a binocular microscope. (There are 8 or 9 soft rays.) In the present context it is the structure of the anal fin that is most interesting. The type specimen of *Macdonaldia challengerii* (Vaillant) has 55 anal spines and the last 20 of these are segmented (see Text-fig. 3c). The last six of these spines, having one or two extra segments, are somewhat more flexible than the rest, but they still have pointed tips. In a specimen of *Macdonaldia rostrata* the transition between “segmented spines” and rays is less distinct. If the last “segmented spines” are judged to be spinous on account of their rigidity and pointed tips there are 29 anal spines (*sensu lato*). Each of these has a posterior median ridge which contributes





to its rigidity. But beyond the last of such spines come several "rays" without this ridge yet still with pointed tips.

If a spine is judged to be a rigid, pointed ray with no trace of segmentation or a double structure, the "jointed spines" of notacanthus must be excluded. But are they soft rays? (To a predator at the pointed end they may deter just as well as "true" spines.) A soft ray is a flexible, jointed structure, made of left and right, closely apposed series of lepidotrichia. If a soft ray is unbranched, the tip is not sharply pointed and rigid. The spines of notacanthus with some signs of segmentation lack these features, except that the innermost pelvic spines may sometimes be forked. Rigorous adherence to a spine-soft-ray polarity might mean finding a new name (such as pseudacanthus) for the segmented spines of notacanthus. If a name must be given, "pseudacanth" would then cover every gradation between a soft ray and a spine. A third category might have some use in taxonomy but the salient feature is the transition from spines to soft rays in the pelvic and anal fins. There can be no better living illustrations of how some spines (*sensu stricto*) may have arisen. (When young notacanthus become available, a study of fin development should be illuminating.) In the present context this transition is further evidence that the spiny fins of notacanthus are not very different in nature from their homologues in the Halosauridae. [It is also significant that the number of spines in these fins, particularly in the anal fin, may vary considerably within one species (see, for instance, Matsubara, 1938).]

If spinous rays have always had soft-rayed precursors, this transmutation, which involves the suppression of the twin structure, jointing and branching of the lepidotrichia, has occurred several times in the evolution of the teleost fishes. But no one can be sure that spines had no more than this one kind of origin. [Woodward (1942) suggested, for instance, that fin spines might be modified fulcral scales.] Concerning the development of spines, François (1959) has shown that the spinous dorsal rays of *Pterophyllum* arise from a median and *unpaired*, blastematous mesenchyme in the fin fold. Some fin spines might thus have always been spines.

FIG. 3. (a) The transition between spiny rays and soft rays in the anal fin of *Notacanthus bonapartei* ( $\times 3$ ). The figure shows 4 spines that bear signs of segmentation, and they follow a plain spine. The last spine is a single structure, not consisting of two halves, as does the first soft ray.

FIG. 3. (b) The pelvic fins of *Notacanthus bonapartei* ( $\times 3$ ). The left fin (right in the figure) bears three spines: the right fin has two. The innermost spines are not only partially segmented, but are branched as well.

FIG. 3. (c) The transition between spiny rays and soft rays in the anal fin of *Macedonia challengerii* ( $\times 5$ ). The numbers above the rays refer to their position in the fin. After robust and ridged spines (like 28, 29 and 30) come partially segmented spines (like 39, 40 and 41), which have a single structure. Following these came rather flexible rays (like 60, 61 and 62) with more segments and a double structure, but with pointed tips. A typical soft ray (70) is shown on the extreme right.

Yet in a classic type of percomorph fish, the striped bass (*Roccus saxatilis*), the third anal spine develops from the first segmented soft ray. Mansuetti (1958) has found that this ray loses its jointed structure, becomes ossified and fuses into a typical spine. He also found that the third anal spine of certain haemulids develops in the same way; while Ginsburg (1953) had already described a similar condition in the scorpion-fish, *Pontinus longispinis*. However, this phenomenon seems to have been first noticed in *Mugil*.

After reviewing the paper by Ryder (1886), Mansuetti gives the following apt summary of present knowledge concerning the development of spinous rays. "Thus he (Ryder) and Goodrich allude to three types of spine formation: (a) an outgrowth of a hollow, terminally blind sac of the outside cellular wall of the embryo, exclusive of embryonic ray formation; (b) development from left and right halves of fin rays which fuse together into a hollow rod in the mid-line at an early stage, which is possibly the type of origin of first and second anal rays in the striped bass, and (c) development from a well formed soft ray through the processes of structural change and ossification and this, of course, is how the third anal spine formed in the striped bass". Fin spines may also arise, as already stated, from an unpaired *anlage* in the embryonic fin fold (François, 1959).

But, unlike notacanth, no grown percomorph fish is known to have fin spines that still display some signs of their origin from soft rays. Such tell-tale traces seem to be rare in spiny-finned members of (typically) soft-rayed groups. However, signs of articulation can be discerned in the pungent fin spines of the spiny-rayed (plagopterine) cyprinid fishes (Miller and Hubbs, 1960). Perhaps a careful scrutiny of all manner of spinous rays will reveal other such instances (see Hubbs, 1944). There is also relatively little knowledge concerning the development of spiny rays. When both aspects have been more thoroughly explored a better appreciation should be gained of one of the outstanding events in the history of fishes; the evolutionary development of spiny-rays. After all, more than half the species of living fishes have fin-spines of some kind or other.

The halosaurs and notacanth are very alike in swimbladder bauplan. As well-preserved specimens of *Notacanthus bonapartei* were available, some description of the swimbladder of this species will first be given. The sac occupies the posterior two-thirds of the body cavity and starts just behind the liver. As Günther (1887) observed, the swimbladder of *Notacanthus* is forked at the front into left and right cornua. The two retia mirabilia originate towards the front of the left fork and they extend backwards within the walls of this structure as far as its junction with the main cavity of the swimbladder. This left-hand fork, as Günther also saw, may have a duct-like forward extension: "A pneumatic duct can be traced for a short distance from the end of the left corner, but is soon lost and does not appear to reach the oesophagus". But Lozano Cabo (1952) stated that the swimbladder of *Notacanthus bonapartei* was united with the oesophagus by a pneumatic duct. Maul (1955) also found a pneumatic duct in this species, but judging from his drawing this may be the inner lining of the duct. Tucker and Jones (1951) figure a pneumatic duct in a large specimen of *Notacanthus phasganorus*. But in no instance is there any evidence of the duct remaining completely open in an adult fish. Like nearly

every species of deep-sea fish with a swimbladder, the Notacanthidae (and Halosauridae) are physoclists. Even if the pneumatic duct opens into the oesophagus, as in the parasitic eel *Simenchelys* (Jacquet, 1920) the swimbladder can function as a closed organ, for the gas gland and retia are very well developed. Apart from this, a *Simenchelys* living near the bottom, perhaps at a depth of several hundred metres, is hardly going to climb to the surface to gulp atmospheric air. On its way down most of its acquired buoyancy would soon be lost.

Returning to the swimbladder of *Notacanthus bonapartei*, the left-hand horn, which will now be regarded as an expanded, posterior part of the pneumatic duct, opens into the main swimbladder cavity at a point about two-fifths of the way down the major axis. Around the opening there appears to be a muscular sphincter. The two retia mirabilia (each about 15 mm. in length in a swimbladder from a 335 mm. fish) end at this point, where the capillaries continue straight towards a corresponding area of gas gland, the cells of which are scattered in rather diffuse, meandering patches. The retia are thus unipolar. One rete turns back at the above opening and feeds a gas gland in the right-hand fork, which is simply the forward part of the main cavity. The other rete supplies another glandular area in the middle region of the sac (see Text-fig. 4a).

The resorbent part of the swimbladder appears to be centred in the expanded part of the pneumatic duct. By-pass branches from the blood vessels forming the two retia extend down the anterior part of the expansion and there are certainly many smaller vessels close to the inner epithelium.

The swimbladder of other notacanthids also has this bauplan. The two retia mirabilia in the posterior pneumatic duct of *Macdonaldia challengeri* (type specimen, standard length 394 mm.) are about 17 mm. long. In a 230 mm. *Notacanthus indicus*, taken by the John Murray Expedition off the South Arabian coast, one rete (length 12 mm.) appears to be considerably wider than the other (see Text-fig. 4b). The specimen shows very well the forward continuation of the pneumatic duct, the posterior walls of which contain the two retia. The continuation appears to taper blindly to a point about 10 mm. in front of the origins of the retia. In this specimen I was also able to see that the bulbous part of the pneumatic duct is well supplied with blood vessels, which suggests that this is indeed the resorbent part of the swimbladder.

The bauplan of the halosaur swimbladder is very like that of the notacanthids. I have examined three species, *Halosaurus oveni*, *H. parvipennis* and *Aldrovandia affinis*. In *H. oveni* the origin of the two retia mirabilia is a few scale rows behind the base of the pectoral fins and the main sac extends down most of the body cavity. The specimen dissected was 337 mm. in length: the two retia spanned about 20 mm. They are housed in the walls of a posterior, expanded part of the pneumatic duct, which is to the right of the sac, and they end at the (ventral) opening of the duct into the main cavity (see Text-fig. 4c). The pneumatic duct continues forward of the retial origins, and it may end, as Günther (1887) found " . . . in a thread attached to the oesophagus". The retial vein appears to join the hepatic portal system. Each rete supplies a corresponding half of the gas gland. Lastly, there is a short appendix near the front end of the main sac (see Text-fig. 4c), which looks

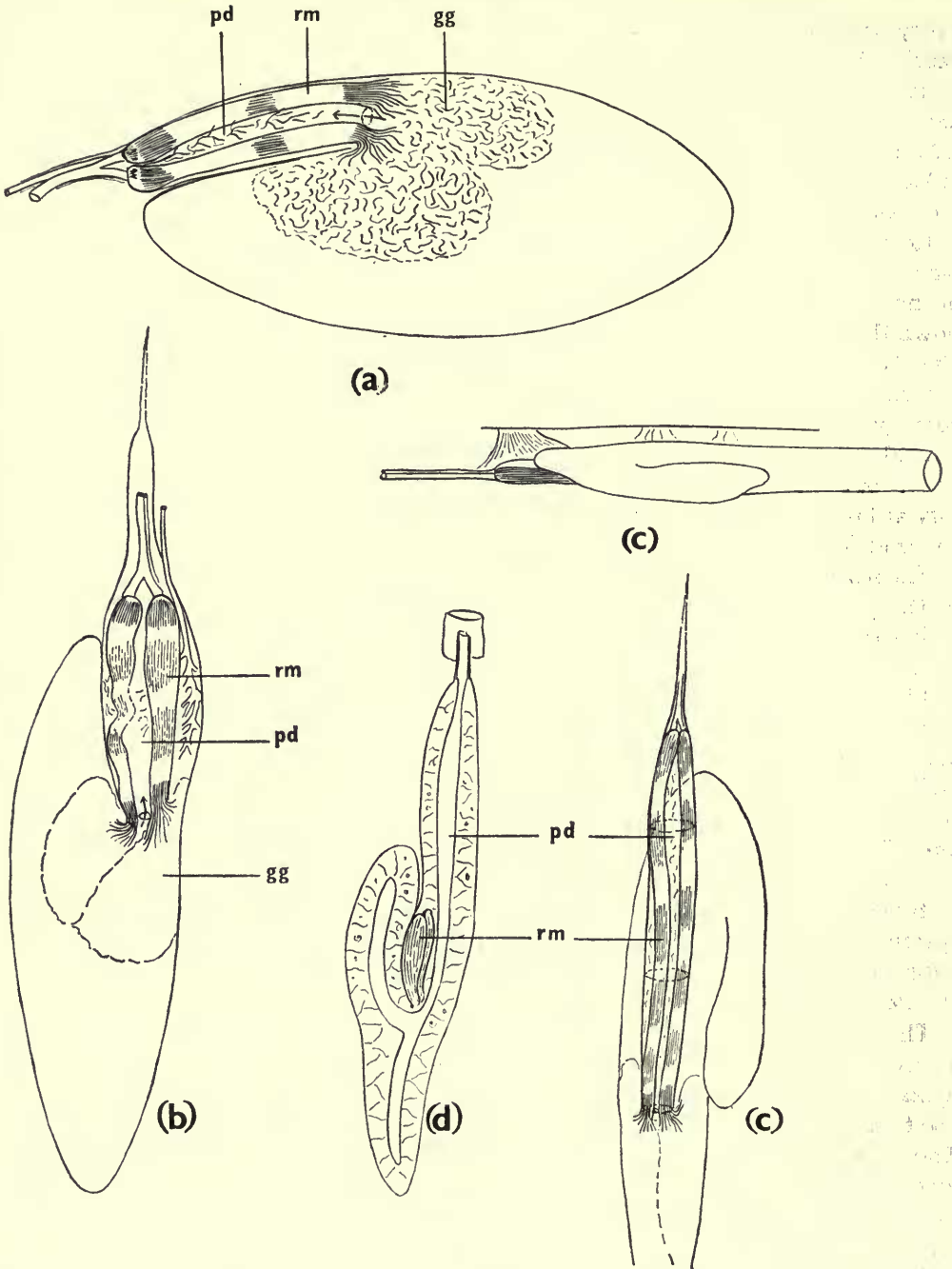


FIG. 4. (a) Swimbladder of *Notacanthus bonapartei*, ventral view ( $\times 2$ ); (b) Swimbladder of *Notacanthus indicus*, ventral view ( $\times 2.5$ ); (c) side view ( $\times 2$ ) and ventral view ( $\times 2.5$ ) of the swimbladder of *Halosaurus oeni*; (d) developing swimbladder in an elver of *Anguilla anguilla* ( $\times 12.5$ ). gg., gas gland; rm., rete mirabile; pd., pneumatic duct, the walls of which are highly vascular.

as if it might compensate for any asymmetry in buoyancy due to the off-centre placing of the rete-containing section of the pneumatic duct. But this could only be decided by examining a freshly caught fish with a properly expanded swimbladder.

Except for the absence of this appendix, the structure of the swimbladder in *Halosaurus parvipennis* and *Aldrovandia affinis* is essentially similar to that of *H. oveni*. The lengths of the two retia are about 20 mm. both in an *A. affinis* (length of fish 325 mm.) and a *H. parvipennis* (length 260 mm.).

The design of the swimbladder is thus remarkably similar in the Halosauridae and Notacanthidae. We have also seen that the two groups are basically alike in opercular structure and not very distinct in fin structure. If these facts are considered together with other similarities, such as listed by Regan (1929) and Berg (1940), there is good reason for retaining the order Heteromi in the wide sense. The members of this order would thus be the Halosauridae, the Lipogenyidae and the Notacanthidae. Dr. S. Macdowell, who is preparing a section on the Heteromi for the *Fishes of the Western North Atlantic* has also come to this conclusion, and it is interesting that his views are largely based on a detailed study of the skeletal system. I am most grateful to him for allowing me to see copies of the completed parts of his manuscript.

#### THE HETEROMI AND THE APODES

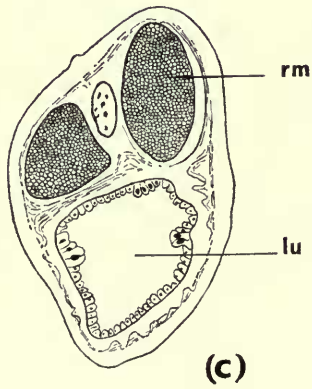
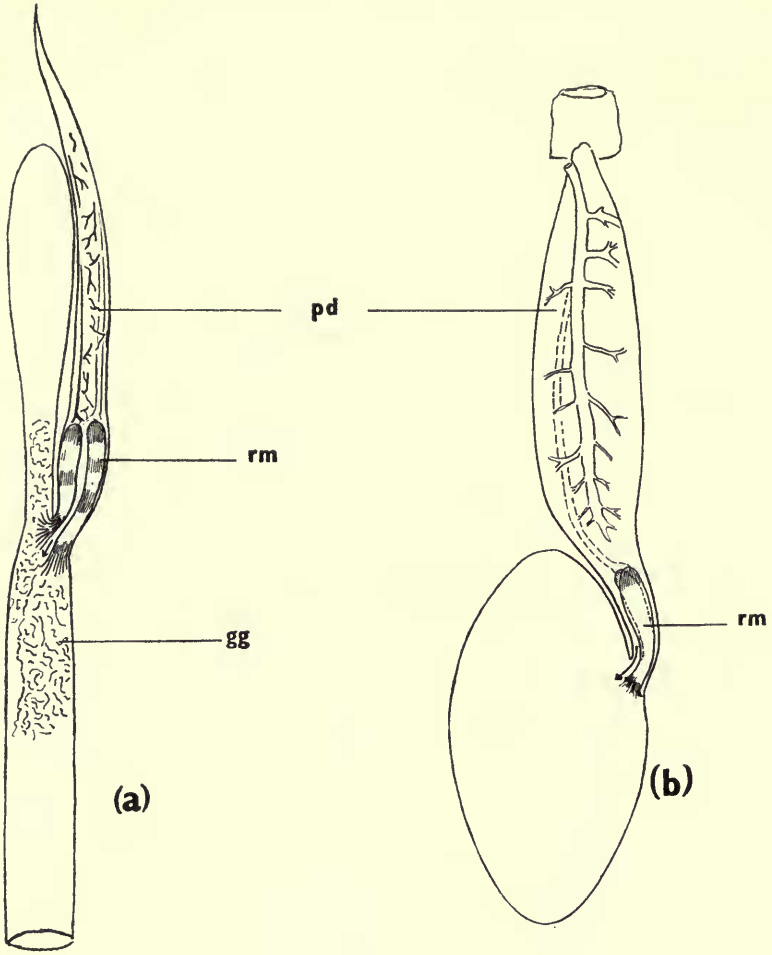
The similar design of halosaur and notacanth swimbladders is not so surprising, but I was less prepared to find that this design is remarkably like that found in eels (Apodes) (see Text-fig. 5). To take the best known instance, the swimbladder of the freshwater eel, *Anguilla* (Woodland, 1911; Fänge, 1953) is like that of a heteromous fish in the following respects :

- (i) An expanded, posterior part of the pneumatic duct forms the resorbent part of the swimbladder.
- (ii) The walls of the duct contain two retia mirabilia.
- (iii) The retia mirabilia end where the duct opens into the main cavity of the swimbladder.

This kind of swimbladder is also found in *Conger conger*, *Myrus vulgaris*, *Ophichthys imberbis* and *O. serpens*, except that the third species appeared to have but one rete mirabile (Woodland, 1911).

Again, *Simenchelys parasiticus* has much the same type of swimbladder, but judging from Jacquet's (1920) figures, the pneumatic duct seems too narrow to form an efficient resorbent surface. Perhaps this is centred in the forward bulbous part of the main cavity, which according to Jacquet is thin-walled.

A forward, somewhat bulbous part of the swimbladder is also found in *Synphobranchus* (see Text-fig. 5a) and this connects with the main, posterior chamber through a rather narrow neck. Beyond this neck is the opening of the pneumatic duct, which is on the left side of the posterior chamber. The more expanded, posterior part of the duct contains two retia mirabilia, each about 10 mm. in length. The pneumatic duct continues forward well beyond the origin of the retia and finally seems to taper to a thread, which is attached to the roof of the body cavity just



below the kidneys. (This attachment is just ahead of the extremity of the bulbous section.) The resorptive part of the swimbladder appears to be confined to the widened, posterior part of the pneumatic duct. Well forward of the origin of the retia, the walls of the duct contain many blood vessels.

The only notable difference between swimbladder structure in the Heteromi and Apodes is that the latter have bipolar retia mirabilia, whereas the retia of the hal-saurs and notacanthids are unipolar (see Marshall, 1960 for further discussion of these two retial types). But the retia of *Synaphobranchus* are unipolar and the same may be true of *Simenchelys*, judging from Jacquet's (1920) figures. Bipolar retia are clearly not an invariable feature of eel swimbladders.

The swimbladders of the Apodes and Heteromi thus conform to a strikingly similar bauplan, which suggests that the two groups might have evolved from a common ancestor. As we see them today, both types of fishes are decidedly specialized, but certain other likenesses might be expected if they really had a common origin.<sup>1</sup> Relevant similarities in form would seem to be as follows :

- (1) Both orders consist of elongated, long-tailed fishes with a spine composed of many vertebrae (with parapophyses not fused to the centra).
- (2) Upper intermuscular bones (epineurals) and pleural (lower) ribs are developed (some eels also have epipleural (upper) ribs).
- (3) The scales are cycloid (although most eels are scaleless).
- (4) There is a long, many-rayed anal fin (reduced in certain eels) and the pelvic fins are abdominal [in eels pelvic fins are only known in the fossil genus *Anguillavus*, which had eight-rayed pelvic fins. (c.f. 8-10 rays in the Heteromi)].
- (5) Head features. The eyes are covered by "spectacles" formed from the skin of the head. The upper jaw is bordered by the premaxillae and maxillae (in eels the premaxillae coalesce with the mesethmoid and sometimes with the vomer : in the Notacanthidae only a small backward part of each maxilla is included in the gape). There is also a marked resemblance between the form and arrangement of the frontals and parietals, the latter meeting in the middle line of the skull. There is then no contact between the frontals and the supraoccipital.
- (6) There are no oviducts.

Discussion of the differences between the heteromous fishes and the eels would be largely concerned with their specializations. In eels these are : the highly modified respiratory and opercular systems (entailing the separation of the pectoral girdles

<sup>1</sup> Do heteromous fishes have a leptocephalus larva ?

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FIG. 5. (a) anterior part of swimbladder of *Synaphobranchus kaupii*, ventral view ( $\times 2.5$ ); (b) ventral view of swimbladder of *Anguilla anguilla* ( $\times 2$ ); (c) a transverse section through the pneumatic duct of *Anguilla*, showing the two *retia mirabilia* in the walls. The epithelial lining of the lumen is shown (after Woodland, 1911). gg., gas gland; lu., lumen of pneumatic duct; rm., rete mirabile; pd., pneumatic duct, with highly vascular walls.

from the skull and the loss of the post-temporal bones); the loss of scales and the pelvic fins; the firmly built skull, including the fusion of the premaxillae to the ethmoid region; the modified suspension and variable development of the palatopterygoid bones, etc. (see Gosline, 1959 for an interesting discussion of eel specializations in relation to the habits of these fishes).

The more obvious features of the Heteromi are: (1) the projection of the snout beyond the mouth; (2) the development of a forward, "rostral" extension of the ethmoid region; (3) the spine-like process of the maxilla; (4) the absence of a tail fin; and (5) various skeletal reductions, e.g. the absence of the mesocoracoid, postcleithrum, orbitosphenoid and basisphenoid.

Returning to the similarities between the two orders, the eye "spectacles" could be convergent features, necessary protections for the eyes of rooting and burrowing fishes. (The firm build of the fore part of the skull in eels and the rostral extension of the heteromous fishes are also likely to be adaptations for burrowing.) But even disregarding this probable optical convergence, the eels and Heteromi still have numerous common features, underlying, as it were, their more obvious specializations. Undoubtedly the most marked resemblance is in swimbladder bauplan. If one knew that this was no more than an instance of convergence, the other similar characters would not readily lead one to suppose the two orders could have had a common origin. But there is such a close and detailed resemblance in swimbladder structure (see pp. 261-262), and, moreover, this bauplan is unique to these two orders.

To continue this line of thought, it will be relevant to look at some of the uses that can be made of swimbladder structure in the major classification of teleosts. The Isospondyli are a good starting point, and not simply because this order includes some of the most primitive species.

Considering first the Clupeoidea, and beginning with *Chirocentrus*, Ridewood (1905) regarded it as a clupeoid fish. Indeed, he concluded thus: "*Chirocentrus* agrees so closely in the structure of its skull with the Clupeidae, that appeal must be made to other organs of the body for evidence to support the views of those who would make of it a distinct family, the Chirocentridae . . .". Berg (1940), however, separates *Chirocentrus*, even making it the basis of a new suborder of Isospondyli (and quotes Jacobshagen to the effect that teleosts have no spiral valve in the intestine, such as *Chirocentrus* is said to possess). But *Chirocentrus* has a swimbladder that is very like that of a clupeid. Each tubular extension to the (appropriate) inner ear ends in two vesicles that are lodged in prootic and pterotic bullae: the pneumatic duct opens into the stomach (Ridewood, 1905; Srivastava, 1956). Moreover, in *Chirocentrus* elongated branches of the lateral line canals run over the surface of the gill cover bones; a character that is thus not uniquely clupeid. Indeed, Clausen's (1959) description of the head canals in *Denticeps* reminds one of the clupeid branching system. After remarking that the detailed pattern of ramifications is unique among teleosts, Clausen does state that there is some similarity to the condition found in *Clupea*. In view of this it is interesting to find that the pneumatic duct enters the stomach and that swimbladder diverticula are present in the ears as in the clupeids.

The clupeids and *Chirocentrus* are thus quite closely related, and in two striking



respects, bauplan of swimbladder and lateral line system, they are more than suspiciously like *Denticiceps*. There may even be good reason for putting the Denticipitidae, the Chirocentridae, and the Clupeidae in a division Clupeiformes<sup>1</sup> of the suborder Clupeoidea. As already implied, the characters of the division could reside in the stethoscopic type of swimbladder (with an opening into the stomach) and in the fine system of lateral line branches over the gill cover bones. Moreover, the clupeids and *Denticiceps* (but not *Chirocentrus*) have scutes along the mid-ventral line of the trunk, while in *Chirocentrus* and the clupeids there is little or no extension of the lateral line canals over the trunk.

If this be admitted, it would then be sensible to group the Elopidae and Albulidae in the Elopiformes and the Alepocephalidae and Searsidae in the Alepocephaliformes. The elopiform fishes have, *inter alia*; a leptocephalus larva; numerous branchiostegal rays (except in *Pterothrissus*); parietals meeting before the supraoccipital; a subtemporal fossa, and pelvic fins with 9 to 15 rays. [*Elops* and *Megalops* have a large gular plate and there is a rudiment of this bone in *Albula*.]

It is less easy to define the Alepocephaliformes, but there can be little doubt of the relationship of the two families. They lack a swimbladder and generally have small pectoral fins that are placed low down on the shoulders. Photophores are present or absent and there is a tendency for the loss of scales on the head. The dorsal fin nearly always arises behind the mid-standard length, either overlapping the anal fin or being opposed to it. Nearly all alepocephalids and searsids have 7-9 branchiostegal rays.

Turning to the Stomiatoidea, one gets a decided impression that they form a natural group, but it is by no means easy to find diagnostic features. However, a good many species have retained a swimbladder, and, as I have said elsewhere (Marshall, 1960), this has a unique kind of bauplan: it is paraphysoclistous with a single, bipolar rete mirabile at the posterior end.

The deep-sea salmonoids also have a characteristic kind of (euphysoclistous) swimbladder containing numerous micro-retia. Again, study of this organ reinforces the idea that these fishes belong to a natural group, which I suggested might be the Argentiniformes (Marshall, 1960). The other salmonoids (Salmoniformes) have an open swimbladder with a short pneumatic duct at or close to the anterior end of the sac. One species (*Coregonus lavaretus*) is known to have micro-retia (see Fahlen, 1959), but these seem to be absent in *Salmo*. (Close study of a range of salmonid swimbladders would be particularly interesting.)

Thinking of this tendency in salmonoids to develop a diffuse retial system, it is interesting that *Esox* also has micro-retia (see Corning, 1888). One is reminded of Berg's (1940) contention that the esocoid fishes originated from osmeroid fishes at the end of the Cretaceous period. Perhaps this parallelism in an unusual kind of retial structure adds point to Berg's idea. At all events, and ranging further afield, it might well be worthwhile to make a survey of swimbladder structure in the "salmonoid" fishes of the Southern Hemisphere (Galaxiidae, Retropinnidae

<sup>1</sup> The use of the ending "-formes" is surely more appropriate to a division than to an order. Clupeiformes is too specific a name for an order. To take but a few instances, *Opisthoproctus*, *Macristium*, *Phractolaemus*, *Cromeria* and *Gymnarchus* hardly impress one as being "clupeiform".

and Haplochitonidae). On the one hand, they seem to have certain affinities to the esocoid fishes, and, on the other, to the northern salmonoids (see Gosline, 1960). cursory examination of the swimbladder of *Retropinna retropinna*, *Haplochiton zebra* and *Galaxias attenuatus* certainly shows that the position and gross features of the pneumatic duct are similar to those in salmonoids and esocoids. But *Retropinna* has a two-chambered swimbladder, and in the other two species the pneumatic duct opens into the stomach. Closer study is obviously needed.

The mormyroid and notopteroid fishes also have a distinctive swimbladder. In the former each ear is closely coupled to a vesicle derived during development from a bifurcating, forward extension of the sac. Yet this is one of many diagnostic features of a remarkable group of isospondylous fishes. Concerning the notopterids, Dehadrai (1957) has resolved certain ambiguities in the early work of Bridge (1889) on *Notopterus borneensis* and studied other species. Each anterior caecum of the swimbladder is associated with the anterior part of the sacculus (not with the utriculus, as formerly supposed). Apart from this, there are several other distinctive features of the notopterid swimbladder, such as the sub-spherical sac and the ventral diverticula.

Now according to Berg (1940), the Hiodontidae are notopteroid fishes, but the differences between this family and the Notopteridae seem more impressive than their similarities. After discussing the skeletal features of both groups, Ridewood (1904) concluded that: "Although in *Notopterus* and *Hyodon* there are vesicles of the swimbladder on the lateral face of the otic region of the cranium, it does not necessarily follow that these structures have had a common origin. The connection between the swimbladder and the ear must not be relied upon too implicitly as indicating close relationship between such fishes as possess it". But a more significant point is that reliance can only be given to structures that are closely similar in all essential respects. [The Clupeiformes (*sensu stricto*) may be taken as a paradigm of this contention.] Indeed, Ridewood (1904) found that each otic connection in *Hiodon* is made by a "great vesicle of the swimbladder". The complete description suggests that the *Hiodon* type of auditory coupling is not *closely* like that of a notopterid. In fact, the divergence seems substantial. But once more, what is needed is a careful anatomical study of the swimbladder in *Hiodon*. We might then come nearer to appreciating the systematic position of this interesting genus of fishes.

The Ostariophysii also contain some primitive teleosts. But the order is readily distinguished from the Isospondyli by the two chains of ossicles (Weberian apparatus) linking the ears with the anterior chamber of the swimbladder. The structure of these extra auditory channels are remarkably and closely similar in the characoid and cyprinoid fishes. The Siluroidea might well be regarded as a separate order if it were not for the Weberian apparatus etc. But in all essentials of an intricate mechanism, the siluroids are like the other Ostariophysii. As Chranilov (1929) shewed, there are no trenchant differences between the Weberian apparatus of the cyprinoids and siluroids. One divergence concerns the greater degree of fusion of the anterior vertebrae in siluroids: others involve such structures as the ossa suspensoria of the swimbladder and the details of linkage between the

sinus impar, claustrum and stapes (see Chronilov, 1927, 1929). But the most reasonable conclusion is that this whole elaborate mechanism, particularly the sequence of ossicles and the remarkable modification of the labyrinths, is very unlikely to have been independently acquired by the siluroids.

Turning to the Iniomi, swimbladder structure fully reveals the Myctophidae as a natural group, distinct from the Neoscopelidae and unlikely to have had a stomiatoid ancestry (Marshall, 1960). The Miripinnati also have a unique kind of swimbladder (Bertelsen and Marshall, 1956).

To end, but not complete, this review of swimbladder structure and its uses, both actual and potential, in the classification of teleosts, we may consider the position of the Thoracostei (sticklebacks). That these fishes seem to be most closely related to the Solenichthyes is suggested by certain structural congruences (see Berg, 1940), and the difficulty in placing the genus *Indostomus*. While the armature of the body reminds one of a syngnathid, Bolin (1936) has shown that it is more like the sticklebacks in a number of characters. Whether this genus should be put in its own order or in a suborder of Thoracostei can only be determined by a more detailed study of its anatomy. Regarding the relationship between the Thoracostei and Solenichthyes, it may be significant that both have a euphysoclistous, two-chambered swimbladder. The forward chamber contains one or more retia mirabilia and a gas gland, while the rear chamber is concerned with the resorption of gases. But two chambered swimbladders of this basic type have been evolved independently in a number of distantly related groups of teleosts. Yet again we must turn to the details of structure if we are to make the best use of what is now a possible structural clue to relationships.

Returning to one main purpose of this paper, we have seen that the detailed bauplan of the swimbladder in Heteromi and Apodes gives more than a hint that these two orders may well have had a common ancestor, one that evolved from an isospondylous kind of teleost. Without such structural evidence, this conclusion would not easily come to mind.

A final thought concerns our reactions to skeletons. We are impressed by their solid appearance, their architectonic forms, and their seeming wealth of characters. But soft parts may often be more conservative than hard parts, preserving a basic bauplan that can be put to good use in classification. Bone, after all is related to blood, and next to blood is the most plastic tissue in the vertebrate body. This appreciation, which I owe to Professor A. J. E. Cave, is something to keep in mind. Bone is largely shaped by the form and functional needs of the soft organs. It is, so to say, the servant and not the master of these structures.

#### SUMMARY

Regan (1909) and other authorities considered the order Heteromi to consist of the halosaurs and notacanth, but Berg (1940), following Gill (1889), placed them in two separate orders: Halosauriformes (= Lyopomi) (Halosauridae) and Notacanthiformes (= Heteromi) (Lipogenyidae and Notacanthidae). The main characters distinguishing the two orders are the development of fin spines in the notacanth

(absent in halosaurs), and the (supposed) unusual structure of the gill cover bones in the halosaurs.

While the preoperculum is normally formed in the notacanth, the corresponding bone of the halosaurs is believed to be rudimentary. But Günther's (1887) paper is misleading, the bone called the preoperculum actually being the posterior part of the quadrate. The true preoperculum is well developed, but it is remarkable in bearing a very accentuated flange, which covers the small suboperculum and a club-shaped interoperculum. The flange is extended so as to carry the posterior part of the suborbital lateral line canal, which continues straight backwards instead of curving round the orbit. There is thus no room for the (normal) preopercular continuation of the mandibular canal, the course of which is parallel to the suborbital canal.

In fin pattern and spine formation the Lipogenyidae are intermediates of the Halosauridae and Notacanthidae. There is, in fact, a morphological series in these features (Halosauridae → Lipogenyidae → *Notacanthus* → *Polyacanthonotus* → *Macdonaldia*). Moreover, the dorsal spines of notacanth are not isolated elements, but are parts of a single fin, one with a well-knit framework of basal supporting bones. Careful scrutiny of the fin spines of notacanth also shows that some of the spines (certain of the pelvic spines and the most posterior anal spines) still display signs of segmentation: they have spinous and soft-rayed features. The inner pelvic spines may even be branched in the manner of a soft ray.

This hardly seems to show that the differences between the halosaurs and notacanth are trenchant enough to justify ordinal status for these two groups. Study of the design of their swimbladders reinforces this conclusion. In both groups the swimbladder has a main chamber into which opens a large pneumatic duct, which in adult fishes may taper off to a connection (but not an open one) with the oesophagus. The walls of the expanded, posterior part of the pneumatic duct contain two large, unipolar retia mirabilia, which enter the gas gland at the opening of the duct into the main cavity. The expanded part of the duct is highly vascular and must serve for the resorption of gases. In short, the congruence between the swimbladders of halosaurs and notacanth is very close, which fact, combined with their other resemblances, gives ample indication that they form a natural group and a single order Heteromi.

The design of the heteromous swimbladder is very like that found in eels (Apodes), a design that is unique among bony fishes. Indeed, the resemblances are detailed enough to suggest that the Heteromi and Apodes evolved from a common ancestor, which must have been an isospondylous kind of teleost. While the fishes of both orders are highly specialized, there are a number of (other) common features to support this conclusion, which must, however, be largely based on the bauplan of the swimbladder.

The concluding part of the paper is given to a review of the uses, both actual and potential, of swimbladder structure in classifying the teleosts. A striking instance, but only one among many, concerns the common development of a stethoscopic type of swimbladder in the Chirocentridae, Clupeidae and Denticipitidae. This unique kind of auditory linkage and certain other unusual common features, particu-

larly the extension of lateral line canals over the gill cover bones, could suggest that these three families form a natural group (Clupeiformes) of the clupeoid fishes. Consideration of this and other such instances suggests that soft parts may often be more conservative than hard parts, preserving a basic bauplan that can be useful in systems of classification. Bone, after all, is the servant rather than the master of the soft organs of vertebrates.

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